THE GENERA OF PLUMBAGINACEAE OF THE SOUTHEASTERN UNITED STATES ¹

R. B. CHANNELL AND C. E. WOOD, JR.

IN A PRECEDING PAPER in this series (The genera of the Primulales of the southeastern United States, Jour. Arnold Arb. 40: 268-288. 1959), the Plumbaginaceae were excluded from the order Primulales. However, various authors have associated this family and order (especially through the Primulaceae), on the basis of the pentamerous floral symmetry, sympetalous corolla, obdiplostemony, and unilocular ovary with a single, basal, anatropous ovule. Other authors have treated the Plumbaginaceae as a separate, but related, order, the Plumbaginales. In contrast, Hallier allied the family with the Caryophyllales (Centrospermae), and a recent study by Friedrich (Phyton Austria 6: 220-263. 1956) led to a similar conclusion. Considering evidence from anatomy, floral morphology, palynology, embryology, and cytology (as well as from ecology and geographical distribution), Friedrich placed the Plumbaginaceae in the Caryophyllales as a separate suborder, Plumbaginineae, perhaps derived from near the Phytolaccaceae (which with Achatocarpaceae, Gyrostemonaceae, Tetragoniaceae, Nyctaginaceae, Molluginaceae, and Ficoidaceae constitute his suborder Phytolaccineae). In such a position the Plumbaginaceae are aberrant in the sympetalous corolla, anatropous ovule and straight embryo. The suggestion of Cronquist (Bull. Jard. Bot. Bruxelles 27: 22, 23. 1957) that the family be retained in a separate order Plumbaginales, related to but more advanced than the Caryophyllales, seems to be both flexible and reasonable to follow at the present time.

PLUMBAGINACEAE (LEADWORT FAMILY)

Perennial [rarely annual] herbs or subshrubs [sometimes lianas] of polygonaceous habit, ours with alternate, simple, entire, exstipulate leaves. Flowers complete, actinomorphic, 5-merous, hypogynous, bracteate, often heterostylous, variously disposed, ours racemose to paniculate or in modified cymes. Calyx synsepalous, plicate, prominently 5–10-ribbed [-angled or -winged], the lobes membranous or scarious, showy, persistent. Corolla sympetalous or of nearly or quite distinct clawed petals, marcescent, the

Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium made possible through the support of George R. Cooley and the National Science Foundation. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. 39: 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. 40: 94–112, 161–171, 268–288. 1959, and in the present issue. We are indebted to Dr. G. H. M. Lawrence and Dr. L. H. Shinners for their kind help in connection with the nomenclature of *Plumbago capensis*.

lobes contorted and imbricate. Stamens opposite the lobes of the corolla, epipetalous at the base of the corolla or hypogynous, introrse, the anthers 2-loculed, longitudinally dehiscent, the pollen grains often dimorphic. Gynoecium 5-carpellate; styles 1 or 5, linear; stigmas 5, linear [or capitate]; ovary 1, unilocular, usually 5-lobed or -ribbed, the single anatropous, 2-integumented ovule pendulous from a funicle arising from the base of the locule. Fruit an achene, utricle or capsule, wholly or partly enclosed by the persistent calyx. Seed with a straight embryo and firm crystalline-granular endosperm. Embryo sac tetrasporic, 8-nucleate of several distinctive types. (Armeriaceae.)

A family of ten genera and approximately 325 species, chiefly of semiarid, saline and calcareous situations, of wide geographical distribution, mostly of the Old World, especially the Mediterranean and Central Asiatic regions; a number of species cultivated as ornamentals.

The Plumbaginaceae are distinguished from other sympetalous groups by the combination of obdiplostemony, five styles or style-branches, and unilocular ovary with a solitary basal ovule.

The occurrence over the herbage of two types of epidermal glands which secret mucilage and/or calcium salts is a characteristic feature of the family. Chalk glands are universally present on or depressed below the surface of the leaves and stem, and commonly exude water and calcium salts, the latter finally being dispersed over the surface of the plant by rain. Elevated capitate glands which secrete mucilage occur in various members of the family, but apparently are of more restricted distribution, usually being confined to the leaf-axils and the upper surface of the leaf-bases.

REFERENCES:

- Baker, H. G. Relationships in the Plumbaginaceae. Nature 161: 400. 1948.
- ——. Dimorphism and monomorphism in the Plumbaginaceae. I. A survey of the family. Ann. Bot. II. 12: 207–219, 1948.
- Cytotaxonomic studies in the Plumbaginaceae. (Abs.) Heredity 6: 279, 280. 1952.
- ——. Dimorphism and incompatibility in the Plumbaginaceae. VIII^e Congr. Int. Bot. Rap. & Comm. Sect. 9, 10: 133, 134, 1954.
- Bentham, G., and J. D. Hooker. Plumbagineae. Gen. Pl. 2: 623-628. 1876.
- Boissier, E. P. Plumbaginaceae. DC. Prodr. 12: 617-696. 1848.
- Boyes, J. W., and E. Battaglia. Embryosac development in the Plumbaginaceae. Caryologia 3: 305–310. (1950) 1951. [Review of literature; 6 types of development reported.]
- Dahlgren, K. V. O. Zytologische und embryologische Studien über die Reihen Primulales und Plumbaginales. Sv. Vet-akad. Handl. 56(4): 1-80. 1916.
- D'AMATO, F. Contributo all'embriologia delle Plumbaginaceae. Nuovo Gior. Bot. Ital. II. 47: 349-382. 1940.
- Friedrich, H.-C. Studien über die natürliche Verwandtschaft der Plumbaginales und Centrospermae. Phyton Austria 6: 220–263. 1956. (See also Studien über die natürliche Verwandtschaft der Plumbaginales, Primulales und Centrospermae. 101 pp. Inaugural Dissertation, München, 1954.*)

Maury, P. Études sur l'organisation et la distribution géographique des Plombaginacées. Ann. Sci. Nat. Bot. VII. 4: 1-134. 1886.

Pax, F. Plumbaginaceae. Nat. Pflanzenfam. IV. 1: 116-125. 1889.

PHILLIPS, H. M. Karyology and the phyletic relationships of the Plumbaginaceae. Chron. Bot. 4: 385, 386. 1938.

Schoute, J. C. Observations on the inflorescence in the family of the Plumbaginaceae. Rec. Trav. Bot. Néerl. 32: 406-424. 1935. [Plumbago, Plumbagella, Limonium, Goniolimon, Armeria.]

Sugiura, T. Chromosome numbers in the Plumbaginaceae. Cytologia 10: 73-76. 1939. [Limonium (as Statice) and Armeria; undocumented material

from botanical gardens.]

Тієднем, Р. van. Sur les prétendues affinités des Plombagacées et des Primulacées. Bull. Mus. Hist. Nat. Paris 6: 131-135. 1900.

Volkens, G. Die Kalkdrüsen der Plumbagineen. Ber. Deutsch. Bot. Ges. 2: 334-342. pl. 8. 1884.

WILSON, J. The mucilage- and other glands of the Plumbagineae. Ann. Bot. 4: 231-258. pl. 10-13. 1889-91.

KEY TO THE GENERA OF PLUMBAGINACEAE

Leaves cauline; flowers short-pedicelled, borne singly at the nodes in spike-like racemes; corolla tubular-salverform, at least twice as long as the calyx; style 1, slender, with 5 stigmas.

Leaves radical; flowers sessile, borne singly or 2 or 3 together in secund spikes, these in panicles or corymbs; corolla of distinct or nearly distinct, long-clawed lobes; styles 5, distinct throughout, filiform, each with a linear-clavate stigma.

2. Limonium.

Tribe Plumbagineae Spach

1. Plumbago L. Sp. Pl. 1: 151. 1753; Gen. Pl. ed. 5. 75. 1754.

Leafy herbs or subshrubs of Polygonum-like habit, inhabiting hammocks and waste places, the stems somewhat woody and often greatly elongate, the flowers borne in elongate spike-like racemes or panicles at the ends of the branches and in the upper leaf axils. Flowers solitary at the nodes on short pedicels, each subtended by a bract and two lateral bracteoles; at least some species heterostylous. Calyx tubular, truncate at the base, the 5 ribs beset with prominent capitate-glandular trichomes, the somewhat inequilateral triangular lobes short, the sinuses hyaline. Corolla salverform, long-exserted, the lobes broad. Stamens with long, slender filaments free from the corolla; pollen monomorphic, deeply tricolpate with an ornamentation of coarse, blunt spines. Style 1, slender, terminated by a tuft of 5 linear-clavate stigmas; ovary pestle-shaped, the neck tapering into the style. Capsule included, beaked, dehiscent into 5 thick-textured rigid valves, these sometimes coherent at the base and apex; seed linear-oblong, somewhat pointed. Embryo sac of the "Plumbago" type, lacking synergid and antipodal cells. Type species: P. europaea L. (The name from Latin, plumbum, lead, perhaps alluding to the occurrence of epidermal "chalk" glands, their calcareous exudate imparting a lead-gray color to the herbage.) — LEADWORTS.

A pantropical genus of approximately 20 species, only *Plumbago euro-paea* and possibly *P. capensis* Thunb. found outside tropical and subtropical regions; one species native in our area, two or more cultivated, one naturalized.

Plumbago scandens L. is an erect, decumbent or climbing, somewhat woody plant, confined in our area to the southern portion of peninsular Florida where it grows in shady hammocks, as well as on shell mounds in open situations. It has a wide distribution through the West Indies to Argentina, Bolivia, and Peru, and also occurs from Texas and Arizona southward through Mexico and Central America. The calyx, 8–9 mm. long at anthesis, bears prominent capitate-glandular trichomes along the ribs from tip to base, but is otherwise glabrous; the tube of the white or purplish corolla is 1.5–2 cm. long.

A second species, an erect, often diffusely branched, cultivated shrub, a native of South Africa, has become naturalized along roadsides and in waste places in some areas of southern Florida. The azure-blue (or white) corollas have tubes 2.5-4 cm. long, and the calyces, 10-12 mm. long at anthesis, are pubescent, in addition to bearing the characteristic glandtipped trichomes along the distal two-thirds of each rib. Although it has long been known as Plumbago capensis Thunb. (1794), the correct name for this plant eventually may prove to be P. auriculata Lam. (Encycl. 2: 270. 1786), which was included by Boissier in the synonymy of P. capensis in DC. Prodr. 12: 693. 1848. Lamarck's description may apply to this plant, but the critical characters of corolla and calyx, without which certain identification is impossible, are not mentioned. Plumbago auriculata was adopted by Merrill (Fl. Manila, 361, 1912) without discussion and apparently only on the basis of Boissier's disposition of the name. He has been followed by several other authors, but it seems best to retain Thunberg's very widely known name unless the holotype of P. auriculata can be located and shown to be the plant in question. Plumbago capensis is sufficiently hardy to be cultivated on much of the southeastern Coastal Plain, especially near the coast. Chromosome numbers of 2n = 14 and 16 have been reported for this species. The red-flowered P. indica Thunb., a native of southern Asia, is also cultivated in the southeastern United States. Heterostyly has been reported in both of these species.

REFERENCES:

- Boyes, J. W., and E. Battaglia. Tetrasporic embryo sacs of *Plumbago coccinea*, *P. scandens*, and *Ceratostigma Willmottianum*. Bot. Gaz. 112: 485-489. 1951.
- Dahlgren, K. V. O. Die Entwicklung des Embryosackes bei Plumbago zeylanica. Bot. Not. 1937: 487-498, 1937.
- ——. Heterostylie innerhalb der Gattung *Plumbago*. [*P. capensis*, *P. europea*, and *P. indica*.] Sv. Bot. Tidskr. 12: 362–372, 1918.
- Fagerlind, F. Der Embryosack von Plumbagella und Plumbago. Ark. Bot. 29B: 1-8. 1938.
- HALL, H. Plumbago capensis as a hedge plant. Gard. Chron. III. 123: 140. 1948.

HAUPT, A. W. Ovule and embryo sac of *Plumbago capensis*. Bot. Gaz. 95: 649-659. 1934.

Leinfellner, W. Die basiläre Plazenta von Plumbago capensis. Österr. Bot. Zeitschr. 100: 426-429. 1953.

Loiseleur-Deslongchamps, J. L. A. *Plumbago auriculata*. Herbier général de l'amateur 5: pl. 339. 1821. [Drapiez, P. A. J. Herbier de l'amateur de fleurs 1: pl. 31. 1828, includes the same plate with a different discussion. See also Bot. Reg. 5: pl. 417. 1819; Bot. Mag. 47: pl. 2110. 1820.]

Sayeedud-Din, M. Some common Indian herbs with notes on their anatomical characters: VII. Plumbago zeylanica Linn. Jour. Bombay Nat. Hist. Soc.

42: 599-601. 1941.

Tribe STATICEAE Bartl.

2. Limonium Miller, Gard. Dict. Abr. ed. 4. 1754, nom. cons.

Acaulescent herbs of Rumex-like habit, with tough, thickened caudices, petioled radical leaves and naked scapes forming ample panicles or corymbs, the ultimate branches bearing the singly disposed flowers or few-flowered spikelets as secund spikes. Flowers sessile or nearly so, subtended by 3 (or more) ensheathing bracts (the inner the longer); [flowers often heterostylous]. Calyx tubular-funnelform, prominently 5-ribbed, the 5 lobes scarious-hyaline in texture, often with smaller intervening lobes or dentate-erose sinuses. Corolla blue or lavender, the 5 lobes nearly or quite distinct, long-clawed. Stamens with long, slender filaments, epipetalous at the base of the corolla claws or nearly hypogynous; pollen tricolpate, monomorphic [or often dimorphic], ornamented with polygonal areoles surrounded by rods with swollen ends arranged in complete rows. Styles 5, rarely 3, separate, linear-filiform, as long as the filaments; stigmas 5, often dimorphic, ours monomorphic, linear-clavate, papillate; ovary short, cuneate-clavate, truncate. Fruit indehiscent, oblong-clavate, prominently 5-angled, truncate, included or exserted from the persistent calyx, usually capped by the marcescent corolla and the 5 style bases. Seed oblong-ovate, the embryo straight, in mealy endosperm. Embryo sac of the "Fritillaria" type. (Statice L., 1753, partim, emend. Willd. 1809, nom. rejic.) Type SPECIES: L. vulgare Mill. (The name derived from leimonion, the ancient Greek name, presumably from leimon, a marsh.) — SEA-LAVENDER, MARSH-ROSEMARY, CANKER-ROOTS, STATICE.

Approximately 150 species in 16 sections, the genus occurring on all continents; four species in our area, all of sect. Limonium, subsect. Limonium, and in need of re-evaluation.

Limonium angustatum (Gray) Small (not L. carolinianum var. angustatum sensu Blake), with linear-lanceolate leaves ending in cusps 2 mm. long, is known only from the Florida Keys. Limonium obtusilobum Blake, distinguished by the glabrous calyx with obtuse lobes 0.4–0.8 mm. long, is widespread, but apparently uncommon, in Florida. Limonium carolinianum (Walt.) Britt. var. carolinianum, having quite glabrous calyx tubes with lobes 0.5–0.7 mm. long, is distributed in salt marshes along the coast from

Mississippi to Florida, north to southeastern New Hampshire; var. compactum Shinners occurs on the coast of Texas. Limonium Nashii Small, characterized by pubescent calyx tubes with lobes 1–1.7 mm. long, occurs from Louisiana to Florida, north to Newfoundland and the Gulf of St. Lawrence. The latter two species apparently intergrade.

Most species of *Limonium* are dimorphic in respect to pollen structure and stigma morphology. Such dimorphic types are self-sterile but cross-compatible. In L. vulgare heterostyly of the conventional kind is also known. Monomorphic, self-compatible species with a single pollen- and stigma-type are known in a number of sections. Such monomorphism is regarded by Baker as a secondary development within the genus. The European and South American members of subsect. Limonium are all dimorphic, with one exception, L. humile Mill., of Ireland and Britain; all of the North American species, including ours, are monomorphic. Both L. mexicanum Blake, of Baja California, and L. californicum (Boiss.) Heller, are diploid (2n = 18), whereas, on the basis of inferences drawn from pollen measurements, the plants along the Gulf of Mexico and the Atlantic coast are tetraploids.

Balanced chromosome numbers of 12, 14, 16, 18, 28, 36 and 64 (x = 6, 7, 8, 9) have been reported for various species of *Limonium*. Plants with somatic numbers of 27, 32, 33, 34, 35 and 37 are either known to be or are suspected of being apomictic, a condition not yet demonstrated in any of the species in subsect. LIMONIUM.

REFERENCES:

- Arisz, W. H., et al. The secretion of the salt glands of Limonium latifolium Ktze. Acta Bot. Neerl. 4: 322-338. 1955.
- Baker, H. G. Dimorphism and monomorphism in the Plumbaginaceae. II. Pollen and stigmata in the genus *Limonium*. Ann. Bot. II. 17: 433-445, 1953; III. Correlation of geographical distribution patterns with dimorphism and monomorphism in *Limonium*. *Ibid*. 615-627, 1953.
- The agamic complex in *Limonium* (Sections *Densiflorae* and *Dissitriflorae* Boiss.) Proc. 7th Int. Bot. Congr. 329, 330. 1953. [Deals with species outside our range.]
- Limonium in the West Indies. Ann. & Mag. Nat. Hist. XII. 7: 611-614. 1954.
- Blake, S. F. Limonium in North America and Mexico. Rhodora 18: 53-66. 1916.

 Notes on the North American species of Limonium. Rhodora 25: 55-60. 1923. [Includes key.]
- Choudhuri, H. C. Chromosome studies in some British species of Limonium. Ann. Bot. II. 6: 183-217, 1942.
- DE FRAINE, E. The morphology and anatomy of the genus Statice as represented at Blakeney Point. Part I. Statice binervosa G. E. Smith and S. bellidifolia DC. (S. reticulata). Ann. Bot. 30: 239-283. 1916. [Limonium.]
- Salmon, C. E. Notes on *Limonium* I–XV. Jour. Bot. 41: 65–74. 1903; 42: 361–363. 1904; 43: 5–14, 54–59. 1905; 45: 24, 25, 428–432. 1907; 46: 1–3. 1908; 47: 285–288. 1909; 49: 73–77. 1911; 51: 92–95. 1913; 53: 237–243, 325–329. 1915; 55: 33, 34. 1917; 60: 345, 346. 1922; 61: 97–99. 1923.
- SHINNERS, L. H. The Texas species of Limonium (Plumbaginaceae). Field Lab. 24: 105, 106, 1956.

Sprague, T. A. Statice and Limonium. Jour. Bot. 62: 267, 268. 1924. Wangerin, W. Ueber den Formenkreis der Statice Limonium und ihrer nächsten wandten. Zeitschr. Naturw. 82: 401–445. 1911. [Limonium.]

VANDERBILT UNIVERSITY
AND
THE ARNOLD ARBORETUM